ON *BETTONGIA CUNICULUS* OGILBY, 1838 (MARSUPIALIA)

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SUMMARY

An analysis of the characters of a small series of *Bettongia cuniculus* Ogilby from Tasmania is made for comparison with mainland forms of *B. penicillata* Gray and *B. lesueuri* Quoy and Gaimard.

This species was formerly regarded as exclusively Tasmanian in occurrence, and its supposed insularity has tended to minimise somewhat the importance in practical taxonomy of several areas of vagueness and conflict in its description. Since Brazenor (1950) confirmed the Victorian status of the species, as originally claimed by Hall and Kershaw (1917), the necessity for clarifying its distinctions from the well ascertained mainland species has sharpened. A small series of four skins and eleven skulls personally collected in the district of the upper Macquarie River in eastern Tasmania, while inadequate for complete re-description, has prompted the examination summarized below, which may reduce these uncertainties. The comparisons instituted are chiefly with *B. penicillata ogilbyi* of South and Western Australia, and *B. lesueuri* of South and Central Australia; *B. gaimardi* and the eastern form of *B. penicillata*, which may be closer to *B. cuniculus*, have not been available locally.

EXTERNAL CHARACTERS

Rhinarium very coarsely granular, much more so than in *B. penicillata* and *B. lesueuri*, but its upper margin with a backward and upward directed spur, as in the former.

Facial vibrissae weak in comparison with body size, the mysticials reaching 37 mm. as a maximum; the lower rows are white, the upper brown and none black. The supra orbitals may be longer than the mysticials (max. 42 mm.) and are pale brown, as are the genals also with length ranging from 29-36 mm. Black eyelashes are present on both upper and lower eyelids, but are weakly developed. On the lower border of the orbit a crescent of stout black bristles is developed, the longest 17 mm., and there is a similar but weaker series on the upper border; the development of these bristles is very strong in *Aepyprymnus* and falls off in the order *B. cuniculus, B. penicillata, B. lesueuri*. Submentals and interramals were not checked in the fresh material and are incomplete in the skins; the interramals present are two in number, silvery white and from 12-17 mm. long, springing from a common median site about 20 mm. posterior to the mid point of the lower lip.

The manus is much stouter than in *B. penicillata*; the digital formula is $3 > 4 > \text{or} = 2 > 5 > \text{or} = 1$; the 2nd digit is shorter relative to the 3rd than in that species and the 4th is much stouter than the 2nd, and its claw is both stouter and longer, so that its general size superiority over the 2nd is more decided than is indicated by the formula. The claws are straighter and wider at the base and taper more to the point in a superior view than in *B. penicillata* in which they are nearly parallel sided, when seen from above; 3rd claw (maximum) 15·5 mm.; 4th claw 13·5 mm.

Pes stout with short blunt digits and nails; the plantar surface is completely naked as in *Aepyprymnus,* therein differing from *B. lesueuri* and *B. penicillata* in which it is more or less completely haired in the young animal; in colour of integument it is dusky though less so than in *B. penicillata*; granules 14 per cm. under the midmetatarsus, as in *B. lesueuri,* coarser than in *B. penicillata*; nails white.

The tail is stout and in the single example measured has the length about 106 per cent. of that of head and body, as in the Central Australian *B. lesueuri,* and relatively longer than in *Aepyprymnus* and *B.p. ogilbyi.*

DIMENSIONS

The following figures give the dimensions in mm. of an adult male (P^4M^4) measured in the flesh: head and body, 325; tail, 345; chest girth, 180; manus length, 28; nail of 3rd digit, 16; pes, 121; 4th toe, 57; nail of 4th toe, 14·4; ear, 43 × 23; rhinarium to eye, 46; eye to ear, 28; eye (intercanthal), 15; weight, 1590 g.

PELAGE

The texture of the coat is intermediate — crisper than in *B. lesueuri,* much softer than in adults of *B.p. ogilbyi*; it is longer than in either but not denser as to underfur. There is a strong overlay of guard hairs over all the dorsum, except on the nape, where the fur is longer and looser and ruff-like. General colour a pale, strongly grizzled brownish grey, with the head and tail somewhat darker, and the limbs decidedly lighter than the body. In two examples a well-marked pale hip stripe is present, contrary to Thomas's statement.

The composition of the pelage is similar to that of *B. lesueuri* and *B.p. ogilbyi,* but somewhat more complex. Mid-dorsally the main pile of underfur is from 20-23 mm. long; the basal three-quarters of which is Ridgway's blackish plumbeous, a subterminal band of 3-4 mm. wood brown and the points clove brown, not black. Guard hairs vary in length from 27-30 mm. and show some variation in the number of colour bands and their length. The more numerous and stouter have the normal four bands as in the above named species, i.e. 20 mm. plumbeous, 4 mm. sepia, 4 mm. ivory shading to buff and sepia, and 5 mm. sepia. The minority are more slender and the ivory band is split into two by interposition of a very narrow, dark sepia band. There is also a sparse representation of a 3rd category of very stout, all dark guards, reaching 36 mm. and medium sepia. The resulting external colour dorsally is a pale, strongly grizzled drab — the pallor due largely to the blend of ivory and ash buff, which is not much darkened by the overlay of weak sepia points. The colour is warmer on nape and crown and slightly paler on rump. *Ventrum,* basally deep plumbeous, externally greyish white washed lightly with yellow buff. There are two piles—the underfur of 23 mm. ca. in which the basal half is plumbeous and the rest creamy white and the sparse guard hairs of 30 mm. in which the basal ⅝ths is plumbeous, median ⅛th sepia and terminal ⅜ths creamy white. The *sides* are slightly paler than the dorsum, the subterminal colour being reduced to tilleul buff as on the rump. The *head* is slightly darker than the mid back with a small variable area on the muzzle bistre. The *ear* backs are well furred a pale tawny olive, lighter than the head, but variably darkened on the margins; inner surfaces a pale buff; antitragoid tuft not conspicuous. *Fore* and *hind limbs* like the sides externally, but less grizzled; internally, like the ventrum. *Manus* and *pes* much paler than in the forms of *B. lesueuri* and in *B.p. ogilbyi*; a uniform greyish white, very faintly tinged with buff. *Tail* with the dorsal hairing proximally

more erect than in the species named; colour distribution much as in the latter but with the proximal russet areas dulled to buffy drab, gradually darkening to blackish brown over the crest which may occupy ⅓ of the length of the tail and reach 25 mm.; in two specimens the terminal 12 mm. is pure white; the crest is less defined than *B.p. ogilbyi* and its darkest parts are still grizzled with white; the lateral surface is buff fading to buffy white on the ventral surface.

Three of the skins examined were taken in mid-winter and the other in mid-summer, but though they show slight differences in general warmth of colour, degree of grizzling and density, these are not obviously related to a seasonal or sexual factor.

In comparison with *B. lesueuri* and *B.p. ogilbyi* the pelage of *B. cuniculus* is generally conspicuous for pallor; its lighter examples are decidely paler, colder in tone and more conspicuously grizzled than either of these. Its darker variants approach them in colour, but have the further distinction of a much longer pelage, a ruff on the nape, and near white hands and feet. The diagnostic value of the hip stripe is doubtful.

CRANIAL CHARACTERS

In the 11 skulls examined, 10 are fully adult at the P^1M^4 dental phase and one is subadult and at the tooth change. The series is more uniform both metrically and non-metrically than any other *Bettongia* group recently examined (1958), the mean variation in 20 linear dimensions being 9 per cent.

The skull is the largest of the genus, the range of its chief dimensions overlapping the maxima for *B.p. ogilbyi* and *B. lesueuri* or showing a plus clearance; with an average deviation of the mean values of + 7 per cent. from those of the former. The mean displacement volume is 66 cc. as against 64 cc. for *B.p. ogilbyi* and a range of 53-64 cc. in three populations of *B. lesueuri* recently studied. The ossification is light – the mean adult weight of the prepared skull being 16 g. as in the smaller *penicillata*; its surfaces smooth and with muscular ridging even more reduced.

In general outline (Pl. 1, Fig. A-E) the skull is close to *B.p. ogilbyi* with which comparison is chiefly made hereunder. The breadth/length ratio is ·54-·57 (·55); the rostral index is ·41-·43 (·42), and the facial index 223-241 (232).

The rostrum is conical and steeply tapering, but shallower. The proportions of the nasal bones are much the same, but the expanded portion is more extensive and its posterior margins bowed backwards and gently rounded at the corners, and commonly just reach or slightly exceed the interorbital line. The zygomatic arches slightly wider anteriorly, their maxima at or anterior to the midpoint. Interorbital space relatively still wider, remaining quite parallel sided in the oldest skulls available, its concavity rather greater and its edges smooth and rounded. Temporal crests very weakly developed; the interparietal persistent and constant, sharply triangular not semilunar nor crescentic.

In lateral aspect the premaxillae usually make a smaller contribution to the wall of the orbit than in *B.p. ogilbyi*, but with wide variation in the extent of the premaxilliary and maxilliary suture with the nasals. The orbital plate of the lachrymal is very large and the maxilliary process below it, correspondingly reduced, sometimes to a mere splint and in three cases to extinction. In these latter skulls the lachrymal articulates directly with the palatine as in *Potorous* and *Onychogale* and many polyprotodonts. This feature is a good distinction of *B. cuniculus* from *B. lesueuri* and *B. penicillata*, in which as in most Macropodidae the orbital process of the maxilla is a substantial squarish element frequently more than half the area of the lachrymal and sealing off the latter from

contact with the palatine. The zygomata are weak and shallow as in *B.p. ogilbyi*. The supratympanic canal is not completed by bone, though the process of the squamosal which is chiefly responsible for the closure in *B. lesueuri* is strongly developed. The squamosal frontal contact on the temporal wall is constant.

The structures of the palate are generally similar, such proportional differences as occur being caused chiefly by the different character of the secator P^4 and the greater parallelism of the molar rows. The anterior palatal foramina are both absolutely and relatively larger, and the breadth of palate at M^2 also — the latter averaging 20 per cent. of the basal length. The diastema and the posterior vacuities are relatively shorter, the latter reaching to about the middle of the anterior lobe of M^2; they are equally broad and are almost entirely invested by the palatine, a small portion of the anterior margin only, sometimes formed by the maxillae; paired satellite vacuities are sometimes developed in the maxillae. The bulla is much smaller, its length averaging about 10 per cent. and its breadth 26 per cent. less than in the smaller *B. penicillata* skull and its volume is probably less than one-half; as in that species, however, when aged, a thin lamella descending from the ectopterygoid margin of the alisphenoid may reach the anterointernal wall of the bulla, roofing over the foramen ovale and its attendant groove to form a closed canal.

The occipital plane is much as in *B. penicillata*, the paraoccipitals and the mastoid process also, but rather stouter and the latter are not always closely contoured to the bulla.

Mandible, comparatively slight, the maximum breadth, breadth of ascending process and depth of ramus below M_2 and breadth of condyle all relatively lower; masseteric fossa and foramen with a similar range of development, but the process of the angle is shorter and more obtuse.

DIMENSIONS

The following figures give the range and approximate mean of the dimensions in a bisexual series of 9 skulls of adults at the P^4M^1 stage: Greatest length, 79·7-84·1 (82·2); basal length, 68·6-72·9 (71·2); zygomatic breadth, 44·0-46·6 (45·4); nasals length, 33·6-36·8 (34·8); nasals greatest breadth, 13·6-16·0 (14·3); nasals least breadth, 7·0-8·3 (7·8); rostrum depth, 15·0-16·0 (15·3); interorbital constriction, 19·0-21·0 (19·6); palate length, 45·6-48·0 (46·7); palate breadth inside M^2, 14·0-15·2 (14·5); anterior palatal foramina, 3·4-4·9 (4·3); diastema, 12·5-14·2 (13·4); bulla length, 12·9-13·4 (13·1); bulla breadth, 6·7-8·0 (7·3); basicranial axis, 20·8-22·2 (21·4); basifacial axis, 48·4-51·7 (50·4); facial index, 223-241 (232); mandible maximum breadth, 39·1-41·4 (40·4); depth of ramus below M_2, 8·5-9·6 (9·0); breadth of ascending process, 12·4-13·4 (12·9).

SKELETAL CHARACTERS

The following data is derived from the complete prepared skeleton of the young adult male, the flesh measurements of which are given above: Vertebrae; cervicals, 7; thoracic, 13; lumbar, 7; sacral, 2; caudal, 22. Scapula length, 44; do. maximum breadth, 21; clavicle length, 25·5; humerus length, 39; do. distal breadth, 13·7; radius length, 45·5; do. maximum breadth, 5·5; ulna length, 55·5; do. maximum breadth (coronoid), 8·0; femur length, 93·7; do. proximal (trochanteric) breadth, 19·5; do. distal (condylar) breadth, 18·0; tibia length, 115; do. proximal breadth (medial aspect), 19·5; fibula length, 112; do. greatest breadth (proximal), 7·9; pelvis maximum length, 88; do. iliac breadth, 51·0; do.

acetabular breadth, 52·6; do. ischial breadth, 50·5; epipubic maximum length, 12·5; do. articular breadth, 7·7.

DENTITION

The semblances of the dentition (Pl. 1, Fig. F-I) are divided, the incisors favouring *B. penicillata*, the premolars *B. lesueuri* with some degree of intermediacy, and the molars combining the crown features of the former, with metrical characters quite different from both; the mean variation in linear dimensions of post-diastemal teeth is 12 per cent.

The incisor rows meet at a somewhat wider angle than in *B. penicillata*. I^1 is a relatively small tooth, its dimensions about as in *B.p. ogilbyi* and decidedly smaller than in *B. lesueuri*. Tate (1948) implies that this tooth is longer in *cuniculus*, though he does not quote dimensions for it, but I cannot substantiate this in the present material. It is comparatively upright and the medial surfaces are separated by a wider interval than usual, and in anterior aspect have an outward (lateral) curvature culminating in eversion of the tips (Pl. 1, Fig. F); dorso-ventral height 4·7-6·6 (5·8); antero-posterior breadth, 2·5-3·6 (3·0). I^2 is larger than in *penicillata* but has much the same proportions; it is much narrower transversely and less rugged than in *lesueuri*. The height of its crown is much reduced in aged skulls, a condition which may exaggerate the apparent height of I^1; antero posterior length, 3·0-3·2 (3·0); transverse breadth, 1·8-2·0 (1·9).

I^3, as represented by the series means, is somewhat shorter dorso-ventrally and longer antero-posteriorly than in either of the above species, but changes in shape of this tooth are so rapid that without more age phases than are available, it is difficult to decide whether this is characteristic of the species or simply of the phase measured. Its general resemblance to that of *B.p. ogilbyi* is close, and in particular there is no inturning of the crest as in *B. lesueuri* and *Aepyprymnus*; dorso-ventral height, 2·5-3·6 (3·1); antero-posterior length, 2·5-3·6 (3·0). I_1 is a larger tooth than in *penicillata* but similarly proportioned; narrower than in *B. lesueuri*; antero posterior length, 12·8-14·0 (13·3) and breadth, 3·2-3·6 (3·3).

The canine is smaller than in *B.p. ogilbyi* and about equal to that in the lower South Australian *B. lesueuri*; its alveolus lies on the maxillo-premaxillary suture which, as Tate has shown, often approaches it obliquely from behind rather than above; dorso-ventral height, 3·3-4·4 (3·8).

Both the 3rd (and more especially) the 4th premolars are much longer teeth than in *B.p. ogilbyi* and in this approximate to the standards of *B. lesueuri*. Their alignment in the tooth rows is normal, the axis in the upper teeth being nearly parallel to the midline of the palate. The profile of the crests is straight or nearly so, though in P^4 when quite unworn, it may show a slight posterior concavity and although the wall is higher anteriorly than posteriorly, the disproportion is much less than in *B. penicillata*. Hysodontism as gauged by the ratio of greatest height (of enamel) to length is intermediate but much nearer to *B. lesueuri*.

P^3 narrower and less bulky than in the other species, its maximum breadth posterior to midpoint and with a constriction at about its anterior ⅓, and its outline as seen from above more elongate and less regularly oval; grooves 5. P_3 is very similar, the length as compared with its opponent, reduced by about 6 per cent. and the breadth and height by about 5 per cent.; grooves 5. The dimensions of a single example of P^3 and P_3 are respectively: length, 5·1, 4·3; breadth, 2·5, 2·4; height (of enamel wall), 3·5, 3·3.

P^4, the secator, is also a narrower tooth than in either *B.p. ogilbyi* or *lesueuri*, but is much longer than in the former, its length overlapping that of the

Central Australian population of *B. lesueuri* which it resembles in general rather closely; its postero-internal talon and ledge are equally variable and may be virtually absent, but the maximum development of these features is less, and it differs in the deeper hollowing of the buccal face below the cingulum. Though the tooth as a whole is nearly parallel to the intermaxilliary suture, there is some torsion of crest, with very slight extraversion of the anterior portion, which is accentuated by wear. Distinct grooves 6 in 70 per cent., 7 in 30 per cent. of examples, but additional vestiges are sometimes present as in all the species. P_4 is similar in its general characters to the upper tooth; its length is reduced by 11 per cent., but its breadth and height are both slightly increased; the overall size reduction is therefore less than in the other two species; a posterior talon and ledge are not developed. Grooves 6 in 30 per cent., 7 in 70 per cent. of examples; they are shorter than in the other species and have a tendency to bifurcate in their lower course and become lost in obscure crenellations of enamel. Range and approximate mean of dimensions in 10 slightly to moderately worn examples of P^4 and P_4 respectively are: antero-posterior length, 7·5-8·9 (8·2), 7·0-7·6 (7·3); breadth, 2·7-3·1 (2·9), 2·8-3·2 (3·0); height (of enamel), 2·9-4·2 (3·7), 3·6-4·5 (4·0).

The milk premolars are larger than those of *B.p. ogilbyi* and *B. lesueuri* but appreciably narrower. MP^1 is about equal in crown area to M^4 and its trenchant antero-external cusp is very strongly developed; much more so than in these two species and almost as in *Aepyprymnus*. MP_4 much smaller, its crown nearly triangular through reduction of the antero-external cusp. Dimensions of a single example of MP^1 and MP_4 are respectively: antero-posterior length, 3·9, 3·5; breadth anterior lobe, 2·8, 2·4; breadth posterior lobe, 3·3, 2·8.

The upper molar rows are very weakly arched, with the anterior interval but slightly greater than the posterior. The metrical characters of the molars of *B. cuniculus* are markedly distinct from those of *B. penicillata* and *B. lesueuri*; absolute dimensions are higher in most categories, the length of Ms 1-3 *in situ*, exceeding the means of the combined South and Central series of *B. lesueuri* by 10 per cent. and the sum of the crown areas by 20 per cent., while the superiority over *B.p. ogilbyi* is still greater.

In relative size as interpreted by the sectional crown areas, the 2nd is invariably the largest molar both above and below, while in the upper jaw M^1 is sometimes smaller than M^3, a condition not seen in the other species examined; M_1 is invariably smaller than M_3. The overall antero-posterior declension in size is also much less than in *B. penicillata* or *B. lesueuri*, the index of reduction being 1·5-2·1 (1·8) in the upper and 1·3-1·7 (1·4) in the lower teeth. The molar formulae and their approximate frequencies in the upper jaw are $M^2 > M^1 > M^3 > M^4$, 70 per cent., and $M^2 > M^3 > M^1 > M^4$, 30 per cent.; and in the lower jaw, $M_2 > M_3 > M_1 > M_4$, 100 per cent.; the range and approximate mean of the crown areas expressed as percentages of those of the first molars are: M^1 (100); M^2 104-123 (111); M^3 90-107 (97); M^4 52-72 (62); and M_1 (100), M_2 117-134 (125); M_3 107-125 (114); M_4 81-96 (88).

In the size relations of upper and lower molars a notable feature is that M^3 as well as M^1 and M^2 is invariably larger than its lower opponent, M_4 alone of the lower series exceeding the upper tooth with a frequency of 86 per cent. Shape differences are also appreciable; there is a general tendency towards narrowing of the molars and breadth > length occurs as a minority frequency in two molars only (M^1, M^2), whereas in *B.p. ogilbyi* and *B. lesueuri* this condition is represented in all molars, and is dominant in four teeth in the former species and in three of the latter. Further, the condition, posterior lobe > anterior

lobe, which is dominant in both M^1 and M_1 of the above species, is lost in M^1 of *B. cuniculus*, but persists in M_1 with a frequency of 100 per cent.

The range and approximate mean of the antero-posterior length, breadth of anterior lobe and breadth of posterior lobe, in the molars of a bisexual series of 11 skulls, is as follows: M^1, 4·2-4·9 (4·5); 4·2-4·8 (4·5); 4·0-4·6 (4·2); M^2, 4·6-5·1 (4·8); 4·5-5·1 (4·7); 4·1-4·6 (4·3); M^3, 4·3-5·1 (4·7); 4·1-4·7 (4·3); 3·6-4·2 (3·8); M^4, 3-3-4·0 (3·8); 3·0-3·9 (3·5); 2·7-3·0 (2·9); Ms^{1-3} (*in situ*) 13·4-14·6 (14·0); and in the mandible: M_1, 4·0-4·5 (4·3); 3·4-3·8 (3·5); 3·5-4·0 (3·8); M_2, 4·6-5·0 (4·8); 4·0-4·6 (4·2); 3·7-4·2 (4·0); M_3, 4·3-4·6 (4·5); 4·1-4·4 (4·3); 3·6-4·1 (3·8); M_4, 3·8-4·3 (4·1); 3·6-3·9 (3·8); 3·0-3·3 (3·2); Ms_{1-3} (*in situ*), 13·1-14·0 (13·5). In examples showing heavy wear on the crowns, interproximal wear between molars is also appreciable, and the value for Ms^{1-3} may fall to 12·3.

The molars are slightly more brachydont than in *B. penicillata* and decidedly more so than in *B. lesueuri* and the working surface occupies a larger proportion of the crown than in either. The crown pattern is relatively undeveloped as in the former, the cusps and lophs being generally low and obtuse, with the longitudinal elements reduced much below the *B. lesueuri* condition; the midlinks well developed in that species and feebly in *B. penicillata*, are absent. The posterior lophs on the upper 2nd and 3rd molars are scarcely developed as continuous transverse ridges, the buccal and lingual cusps being almost completely separated down to base level by a longitudinal median fissure. The anterior lophs of these teeth, and both anterior and posterior lophs of the lower molars nevertheless, although lower, are often more continuous and more extended transversely than in either *B.p. ogilbyi* and *B. lesueuri*.

Accessory cuspules corresponding to those of *B.p. ogilbyi* are very weakly developed on the 1st and 2nd upper molars in two skulls only. In one skull, M^1 in one maxilla is much smaller and simpler than in the other; in all others the posterior molars are structurally and functionally normal bilobed teeth, appearing regularly in the succession. There are no examples of supernumary molars or incisors.

In the single example of the tooth change afforded by the series, P^4 is erupting simultaneously with M^4.

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EXPLANATION OF PLATE 1

Fig. A. Dorsal aspect of the skull of an adult ♂ from the upper Macquarie River, eastern Tasmania. (x 0·9.)
Fig. B. Palatal aspect of the same. (x 0·9.)
Fig. C. Lateral aspect of the same. (x 0·9.) The pterygoid plate is not shown.
Fig. D. Occipital aspect of the same. (x 0·9.)
Fig. E. Lateral aspect of right mandibular ramus of the same. (x 1·0.)
Fig. F. Anterior aspect of upper 1st incisors of the same. (x 4·4.)
Fig. G. Buccal aspect of an unworn P^4 of the right side in another young adult. Same locality. (x 4·7.)
Fig. H. Buccal aspect of slightly worn P_4 of the right side in another young adult. Same locality. (x 4·3.)
Fig. I. The right maxillary tooth change in an advanced subadult from the same locality. P^4 (upper) is simultaneously displacing P^3 (lower right) and MP^4 (lower middle); M^1 (lower left) persisting *in situ*, is represented by its anterior lobe. (x 4·7.)